Art. XIII.—*The Comparative Age of the Recent Crinoid Faunas;* by Austin Hobart Clark.

There is no point of more importance in the study of recent zoögeographic areas than the determination of their relative antiquity. Such a study must necessarily be based upon theoretical grounds; but there appear to be certain principles by which we may, if we are sufficiently cautious, be safely guided. These principles, as here stated, have been worked out chiefly through a study of the crinoids, though they appear to be applicable to the other marine groups, and probably also to many terrestrial forms. They concern the faunas solely in their physiological phylogenetic aspect, disregarding the external influences of immediate environment.

It must be borne in mind that faunal values vary very greatly in each class of animals, and often in the several orders in each class, as a result of varying reactions to physical, chemical and general economic environment. For instance, sessile or fixed animals would in each locality pass through a definite faunal cycle, such as we see indicated by the crinoids. Among pelagic animals, on the other hand, or among animals with a long free-swimming larval stage, faunal areas comparable to those delimited by the crinoids scarcely exist, and where they are indicated faunal cycles cannot be shown with any degree of certainty. This is due to the continual replenishing of areas, either directly or, as it were, by relays of generations, from a distant source, which, at least in some cases, is probably correlated with a back current carrying to the original source the young of animals which for many generations have lived in a distant area. Thus any change affecting the animals in any particular area would be extremely slow in affecting the species as a whole, for it would be dissipated over such an extent of faunal territory that its influence would be largely counteracted before it could acquire any headway.

Many species inhabiting deep or cold water are recognized as the deep or cold water forms or varieties of other species living in shallow water near shore. It is probable that at least in some of these cases the difference may be caused by physiological changes due to a deep or to a cold environment acting upon the developing young of a single generation, something as the color pattern of butterflies is changed by exposure to heat or cold at the time of pupation. If this were true, such deep or cold water species would have no faunal significance, no matter how great the significance of species associated with them might be, for their character and development would not be due to anything inherent within themselves, but would be quite dependent upon the development of the parent species under the more normal conditions.

Every marine fauna is composed of more or less permanently fixed animals (the most strictly sessile being the crinoids), purely pelagic animals, and animals representing all the intermediate stages. Each class probably has a special faunal cycle of its own independent of all the others, and independent of the systematic affinities of each of the species included in it.

Therefore, to apply the principles governing the development of faunas to a given fauna, we must first of all be familiar with the life history of each of the component types, and of the scope of its tolerance to changed conditions, most weight being given to the facts indicated by the most strictly sessile animals and those most intolerant of any change in their environment (among recent forms the crinoids), and the least to those pelagic species which appear capable of existing anywhere.

Faunas, like individuals, species and genera, pass through a period of youth, of adolescence, of maturity, and of senescence.

In a very young fauna the various genera are represented by several species each, and each of these species is very variable; all of the species are near the mean in their respective genera, none being highly specialized and none retrogressive.

Introduced species which become acclimated and thrive in their new surroundings are found to be, where they have been studied, exceedingly variable. This is equally true in regard to fish, birds, mammals, molluscs and insects, and probably holds good throughout the animal kingdom. We have numerous illustrations of this in such animals as have been introduced into North America from Europe, Africa and Asia.

A young fauna is in effect a fauna composed of species all of which are recently introduced, and all of which, maintaining themselves under optimum conditions, with a minimum of parasites and a maximum of food, are able greatly to increase their coefficient of variation.

Such a fauna we appear to have in the Bering Sea. The crinoids of the shallower waters here are abundant, but all the species, which are very variable, belong to the genus *Solanometra*, an intrusion from the antarctic regions. Of the other echinoderms the starfish present a wealth of forms maddening to the systematist; the number of varieties and incipient and valid species produced from the *Ctenodiscus*, *Hippasteria*, *Solaster*, *Henricia*, and other types, is almost incredible. Conditions are the same among the echinoids, and among the ophiuroids, and apparently among many, if not most, other animal groups as well. Yet with all this variability there is but a slight tendency to produce pathological, defective, or unbalanced types, types which depart widely from the genera mean as calculated from a study of the same genera in other areas.

Although the Bering Sea fauna is the nearest approach to a young fauna which can be found, yet there are a few distinctive genera which show an approach to the next epoch of faunal existence.

So far as the crinoids are concerned, the antarctic region is very young; here we have *Solanometra* and *Promachocrinus* (the latter merely differing from it in the doubling of all the radials), each with several very variable species, though none so variable as the Bering Sea representatives of the same group.

Adolescent faunas exhibit a comparative stability of specific types, coupled with the incipient formation of new genera as a result of a growing tendency of the species to depart widely from the generic mean.

The crinoid fauna of southern Japan might be considered as an adolescent fauna; here we find many genera including several species, each very stable and showing comparatively little variation, such as *Catoptometra*, *Comanthus*, *Dichrometra*, *Parametra*, *Pectinometra*, *Thaumatometra*, and *Pentametrocrinus*, while *Erythrometra*, *Nanometra*, *Calometra*, *Carpenterocrinus* and *Phrynocrinus* are not known elsewhere, though the two last, being from deep water, probably occur to the southward.

In mature faunas the species are fixed, save only for the species at the mean of each genus, which always remains variable, and new generic types are found which have become separated off from the parent genera through the suppression of intermediates, or have arisen by discontinuous variation. As a result of the formation of these new generic types, the number of species in each genus is diminished, and the species are found to approach more or less closely the means of the original genera, or the means of the genera newly formed.

The West Indian crinoid fauna appears to be approximately a mature fauna. It contains a number of peculiar genera, such as *Hypalometra*, *Coccometra*, *Leptonemaster*, *Comatilia*, *Microcomatula*, and *Analcidometra*, while almost all of the East Indian genera which occur here have become more or less differentiated from the original stock, forming new genera parallel to the original East Indian types. In several cases single East Indian genera have given rise to two or more West Indian genera, as *Comissia*, from which *Comatilia*, *Microcomatula*, and *Leptonemaster* appear to have been derived, as well as two other genera which up to now have remained undescribed.

Senescent faunas have lost a considerable proportion of the genera which they possessed at maturity; the genera which remain include aberrant species in which certain characters have become greatly exaggerated, giving those species a curiously unbalanced appearance. There is typically but a single

species in each genus; but there may be two or more, each with a different set of characters exaggerated, in which case they are usually treated as aberrant monotypic genera.

The Australian crinoid fauna is a perfect example of a senescent fauna. It includes about fifty species, nearly all of which are remarkable for the grotesque exaggeration of their specific characters. Even in certain wide-ranging forms, as *Comatula solaris*, Australian specimens have their characters greatly increased over those from other regions.

Some examples of this exaggeration of the specific characters which make the Australian crinoid fauna unique are: the secondary development of biserial arms, indicated in *Comatulella brachiolata*, but not known outside of that genus, which is confined to southern Australia; the development of excessively short cirrus segments and pinnules, also peculiar to this genus; the development of very slender cirri in a comasterid, only found in *Comanthus trichoptera* from southern Australia; the development of twenty armed species of the normally ten armed genus *Comatula;* the occurrence of heterotomous arm division, unique among the comatulids, in the same genus; the development of enormous processes on the pinnule segments, seen in *Comanthina belli* and *Oligometra carpenteri*, representing two widely different families; the development of a very large centrodorsal bearing cirri irregularly arranged in a genus of Thalassometridæ, *Ptilometra;* excessive reduction of musculature in the same family, illustrated by the same exclusively Australian genus; incipient suppression of side, covering, and other perisomic plates, seen in the same genus; extraordinary development of interradial plates in adult comasterids, as seen in *Comanthina belli* and *Comaster multifida;* complete plating of the disk, dissociated from the development of side and covering of plates, as seen in *Zygometra elegans*, *Z. microdiscus* and *Z. multiradiata;* greatly enlarged lower pinnules in a zygometrid, as seen in *Z. miciodiscus;* very small lower pinnules in a zygometrid, as seen in *Z. multiradiata;* aberrant zygometrid arm division, as seen in *Z. elegans*.

A pathological fauna may resemble a senescent fauna in its general facies; but in a pathological fauna all the species, besides being aberrant, are excessively variable, which is never the case in a senescent fauna. Pathological faunas occur usually on the limits of faunal areas, or on the boundary between two very different faunal areas, and are composed in the latter of intrusive species from both the adjacent areas. Many of the animals in Massachusetts Bay, at least in the southern part, indicate a pathological fauna. This is shown by a study of the local species of almost any of the echinoderms, which exhibit an unusually large proportion of abnormalities and aberrant variants of all sorts.

Occasionally faunas are found which combine the characteristics of two or more of the stages described above; these are rejuvenated faunas, faunas which have progressed to the extreme point indicated (or perhaps slightly further) and then have been subjected to some change in environmental conditions which has served as a stimulus, and set a greater or lesser part of the fauna some distance back along the phylogenetic faunal path.

Such a fauna we find indicated by the crinoids about the shores of the large East Indian Islands; some of these approach, in the exaggeration of their specific characters, the Australian species, while others are very generalized, with several closely related species. The crinoid fauna of western Europe is also a rejuvenated fauna; it is composed of two genera, *Antedon* and *Leptometra*, both very close to East Indian genera, the former with five species, three highly specialized and two primitive, the latter including two species, one specialized and one more primitive; in each case the more primitive species occur in the Mediterranean.

It is possible to analyze a fauna on the basis of a single character in a group. Let us take, for instance, the character of the centrodorsal in the Comasteridæ. This organ differs in the several genera and species composing the family only in the degree of specialization, the developmental lines being everywhere the same. In some species, as in *Comanthus bennetti*, the centrodorsal always remains essentially as in the young, but increases in size throughout the life of the individual. Usually, however, resorption takes place at the dorsal pole which is gradually planed off, as it were, so that the centrodorsal changes from the primitive hemispherical form and becomes discoidal, the rows of cirri dropping off as the sockets are resorbed. In extreme cases the resorption results in reducing the centrodorsal to a thin stellate plate, without any traces of cirrus sockets, countersunk within the center of the dorsal surface of the radial pentagon.

We may arrange all comasterid centrodorsals in a linear series, calling the least developed (*Comanthus bennetti*) type A, and the atrophied stellate disk D, B, and C denoting intermediate stages.

Now the species of the Australian fauna have centrodorsals which run from A to D, but with especial emphasis on the D; the species of the East Indian fauna also run from A to D, but the emphasis is between B and C; the Japanese species run from A to C, with especial emphasis at B; the West Indian and east African species are confined between B and C. This holds good regardless of the subfamily or genus to which the species may belong, and exactly the same thing may be worked out in regard to other characters in this family, and with other characters in other families.

The recents crinoids of the Australian coasts are evidently senescent; they unmistakably indicate very great age. So complete, in fact, is this senescence that almost every species is affected. The crinoids of Australia came from the northward, from the great East Indian archipelago; but here continual changes in the distribution of the land and sea have constantly rejuvenated the fauna so that none of its component species has been permitted to drift into the peaceful old age so obvious in almost all the species along the Australian shores.

The fossil crinoids of Europe (belonging to genera still existing) appear to be senescent; but they are no more so, if as much, as are the recent crinoids of Australia. Judging from the evidence offered by the recent forms alone, the European crinoids reached the European seas by passage from what is now the Bay of Bengal north of what is now India. It was probably before this that the same genera spread southward from the parent central East Indian region to Australia.

The crinoids of southeastern Africa represent a comparatively young fauna; they must have reached their present habitat by passage southwestward from Ceylon along a land bridge since submerged; but few of them have as yet entered the Arabian Sea.

The West Indian fauna is younger again than that of the southeastern shores of Africa, from which it was derived. It must have reached the West Indies by following a land which extended from Madagascar to the Antilles, north of what is now southern Africa.

The fauna of southern Japan is very young, apparently younger than that of the West Indies.

The central sea connecting the Bay of Bengal with central Europe had an arm stretching northward across Russia. Certain adaptable genera, becoming acclimated, followed this arm northward and gave rise to the present arctic fauna. More recently one of these arctic genera has spread southward over the north Atlantic.

At a considerably later date a connection was formed whereby the East Indian crinoids, becoming slowly acclimated, reached the antarctic regions. There was also a connection between the antarctic regions and southern South America, whereby these forms secured a foothold on the western coast of that continent, spreading rapidly northward to the Aleutian Islands (dipping downward into deep water when passing under the tropics), and thence southward along the eastern coast of Japan, as far as Tokyo Bay.

This antarctic fauna is apparently the youngest of all the recent faunas, and the evidence of youth increases as we go northward along the west American coast.

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